

THE EVOLUTION OF EYESPOTS IN TROPICAL  
BUTTERFLIES IN RESPONSE TO FEEDING ON  
ROTTING FRUIT: AN HYPOTHESIS

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*Abstract.*—A substantial portion of the butterfly species in tropical forests of Central and South America feed primarily as adults, on rotting fruits and to a lesser degree, on moldy (fermenting) sap issuing from wounds in trees. In general, exploitation of fruit frequently occurs on the ground, where volatile odoriferous substances, released in decay, attract butterflies in the three nymphalid subfamilies Satyrinae, Brassolinae, and Morphinae; similarly, sap and hanging injured or rotting fruit are exploited arboreally by several genera of the Nymphalinae. However, a few nymphalines also feed on fallen fruit and experimentally placed fruit baits on the ground. This paper explores in a preliminary way the possible adaptive relations between (1) feeding on the ground versus feeding arboreally, (2) dispersal agents (vertebrates) as opportunistic predators of feeding butterflies, (3) functional role of eyespot markings (eyespot) on the undersides of wings, and (4) impairment of escape behavior of butterflies from intoxication acquired by feeding on rotting fruits. The general thesis is advanced that butterflies become intoxicated in nature from feeding on rotting fruits, and that eyespots increase the margin for successful escape when normal behavior has been impaired. Since fallen fruits ferment quickly, the intoxication of butterflies is greatest on the forest floor and eyespots are most prevalent in the brassolines, satyrines, and morphos, the three groups that thrive here. Very often, feeding takes place in patches of forest floor directly exposed to sunlight, and at times of the day when such exposure is maximized. Under conditions of direct sunlight, eyespot markings are very noticeable. A high selective value is placed on eyespots as an additional line of evasive escape behavior since animals attracted to fallen fruit (for dispersal purposes and feeding on insects) can be predators on butterflies. Eyespots are known to lure pecking and biting away from the body of a butterfly or moth. Alternatively, it is also known that eyespots frighten away animals. Either way, they function to reduce the likelihood of attack on an insect by a vertebrate predator. It is easy to conceptualize how the three groups of butterflies developed similar eyespots as they are closely linked phylogenetically. For the arboreal-feeding nymphalines, eyespots are expected to be less functional as indicated by their conspicuous absence in most species. Such markings are also generally absent from most flower-visiting butterflies. The decomposition of fallen fruits and the yeasting of sap flows are processes that play a major role in maintaining the butterfly community of tropical forests.

As microbes render fruit less savory for vertebrates that act as dispersal agents, they open a feeding niche for butterflies.

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### Introduction

Each year, the lowland tropical rain forests of Central and South America contain collections of fallen fruits from various tree species. Most of these, such as *Coumarouna oleifera* (Leguminosae) are sweet-smelling rotting, fleshy fruits which attract a variety of butterflies, predominately in the nymphalid subfamilies Satyrinae, Brassolinae, and Morphinae (e.g., Young 1972a). Two major features of these interactions between fruits and butterflies are: (a) although the fallen fruit collection can be large under a parent tree, only certain fruits are returned to repeatedly by butterflies, and (b) an individual of a butterfly species participating in the interaction often returns to the site many times over several days or weeks. The observed extension of the proboscis on, or into, the fruit indicates that the butterfly is ingesting fluids seeping from the fruit.

After a fruit matures, it generally falls to the ground where it sits for some period that may be terminated by dispersal away from the area by a vertebrate (Smythe 1970); if such dispersal does not occur, the ripe fruit spoils and begins to rot as a result of microbial action on the fruit wall. Spoilage is usually accompanied by the emission of a sweet or tangy odor from the fruit. At this stage, the fruit becomes a feeding patch for many insects, including butterflies.

The selective advantages for microbe species to attack fallen fruits prior to the onset of dispersal by vertebrates have been discussed (Janzen 1977). Along with the microbes causing the decay, the insects associated with these fruits, including Lepidoptera, are also conceptualized as being in competition with vertebrates (fruit and seed dispersal agents) for the fruit as a food resource (Janzen 1977). Although the feeding on rotting fruits and fermented fruit products by Lepidoptera and other insects has been documented extensively (e.g., Dethier 1947; Frost 1928; Norris 1936; Barcant 1970; Gilbert 1972; Muyschondt 1973a, b; Young 1972a; Gomez 1977 and many others), little attention has been given to the likely ecological consequences of such feeding behavior. The purpose of this note is to call attention to some possible features of these interactions that relate to a predicted loss in fitness resulting from such feeding, and the role of cryptic coloration and behavior of day-flying Rhopalocera in offsetting these effects. These comments are made as an argument for further documentation of these interactions, especially in the tropics.

### Unusual Butterfly Foods

Adults of many temperate and tropical butterflies imbibe juices from ripe fleshy fruit, and rotting fleshy fruits (e.g., Comstock 1895; Young 1972a ). In the American tropics, many forest-dwelling satyrines, brassolines, and morphos, exhibit this behavior (Brown 1972). In addition, many nymphalines visit fresh arboreal sap flows (e.g., Muysshondt 1973a, b). In general, Nymphalinae such as *Anaea*, *Prepona*, *Adelpha*, *Historis*, and *Marpesia* exhibit this behavior. Among the brassolines, genera such as *Caligo*, *Brassolis*, and *Opsiphanes* have been observed to visit rotting fallen fleshy fruits (e.g., Harrison 1963; Young 1972a; Young and Muysshondt 1975). In addition to feeding on rotting fleshy fruits, both under natural conditions and when baited (Young 1972a; Young and Muysshondt 1973; Young 1973; Young and Thomason 1974; Young 1975), *Morpho* has also been seen imbibing fluids from moldy growths on sap flows of fallen trees (Young and Muysshondt 1973 and Fig. 1). Furthermore, *Morpho* feeds on yeasts associated with disposed dairy products in garbage heaps at the edge of forest at the Monteverde farms in Costa Rica (anonymous).

An outstanding morphological feature of the Satyrinae, Brassolinae, and Morphinae, generally absent in the Nymphalinae and of significance in feeding behavior, is the presence of distinctive eyespots on the undersides of the wings (Fig. 1). In addition to being generally absent from the Nymphalinae, including genera that feed arboreally on sap flows, these markings are absent from most flower-visiting butterflies. Owing to the positioning of the wings in a vertical closed position while feeding (Fig. 1), the eyespot markings (eyespot) are exposed maximally to the visual field of an approaching vertebrate. All four subfamilies of fruit-and-sap-feeding butterflies are cryptically colored in terms of the background coloration of the undersides of the wings.

### Spatial Temporal Variation of the Butterfly Community

Owing to the very great diversity and local species abundance of nymphalines, brassolines, and morphos in the wet forests of tropical America, it seems that the exploitation of ripe or rotting fleshy fruits and fermenting sap flows is a significant factor in determining and maintaining this subset of the butterfly community in a forest habitat. The Morphinae and Brassolinae are strictly tropical groups, while most Satyrinae are also strictly tropical (Ehrlich and Raven 1965). Furthermore, the Nymphalinae are relatively far more abundant in the tropics. In southern Brazil, nymphalines, morphos, satyrines, and brassolines reach very high levels of diversity and many members of these groups exhibit little or no seasonal variation in abundance at a locality throughout the year (Brown 1972). Thus the subset of the adult



Fig. 1. Above: live individual of *Morpho peleides*, wild-caught in northeastern Costa Rica. Note vertebrate-type eyespots on the undersides of both sets of wings. Below: *Morpho peleides* feeding on soupy fungal growth on sap issuing from a fallen tree in northeastern Costa Rica. Time of day is late afternoon; eyespots fully exposed while feeding.



butterfly community associated with ripe and rotting fleshy fruits and moldy sap flows is generally active throughout much of the year, and this is also the case for the northeastern tropical wet lowland forest region of Costa Rica (pers. obs.), and presumably along much of the Atlantic watershed region of southern Central America.

Owing to the generally high spatial patchiness of parent individuals of many tree species in tropical forests (e.g., Black et al. 1950), and the seasonality of fruit production in many of these species (Frankie et al. 1974), rotting fallen fruits for butterflies are expected to be a variable resource from place to place, and from time to time at a given place. Thus the butterflies are expected to exploit a succession of fruit species in space and time as availability of each fruit species changes; during periods of peak fruit production of a preferred species, and at places where the fruit is abundant, it is predicted that populations of butterfly species exploiting this food supply will be residential.

Young (1972a) found that individuals of a given species of satyrine, brasoline, or morpho tend to return to the same fruit baits over several days. Observations such as these and others for *Morpho* (e.g., Young 1973; Young and Thomason 1974) suggest indirectly that the food niche of these butterflies is probably narrow at a given time of the year. The observed tendency for individuals to return repeatedly to the same area of fallen fruit or bait each day (e.g., Young 1972a; Young and Thomason 1974) suggests that these butterflies become familiar with certain portions of the habitat where food resources are found; there is less of a tendency to wander through large areas and rather more of a tendency to become localized near food supplies. What the relationships, if any, of such distributional patterns have to locations of larval food plants has not been determined. In general, though, these observations and those of the preceding paragraph suggest that the subset of the tropical forest butterfly community using rotting fruits and moldy sap flows is a fairly predictable collection of species in space and time. Such conditions may increase predation by home-ranging small vertebrates on adults.

### Cryptic Properties of Adult Tropical Butterflies

Cryptic wing coloration in the Lepidoptera evolved as a means of allowing adults to match the surrounding environment (e.g., Wickler 1968). Most of the Neotropical fruit-eating groups such as the morphos, brassolines, and satyrines possess distinct eyespots on the undersides of the wings. These eyespots closely resemble vertebrate eyes, and several of them often occur on the wings (Fig. 1). In direct light, the eyespots are very noticeable to the human observer, while in shade they tend to blend in with the cryptic background hues of the wings, and of the forest floor. It is believed that such markings stimulate pecking by birds away from the body (Blest 1957; Wick-

ler 1968). Such markings presumably lower the risk of an individual butterfly being eaten while resting or feeding with the eyespots exposed to the visual field of predators. These markings, in combination with generally subdued colors and generally motionless posture while feeding or resting, are effective deterrants for vertebrate predators. It is also known that eyespots frighten away some animals, rather than inviting attack (e.g., Hailman 1977). It is not known which of these types of interactions occur in tropical butterflies feeding on the forest floor, but the frequent occurrence of individuals with uncanny symmetrical sections missing from the hindwings in *Morpho* and *Caligo* suggests that these insects are attacked by small vertebrates (reptiles) while feeding or resting.

With a few exceptions, such as *Prepona*, most Neotropical nymphalines lack eyespots. Yet the general coloration of the undersides of the wings is subdued and cryptic; feeding proceeds generally arboreally from moldy sap flows (e.g., Muyschondt 1973a, b). It appears, therefore, that the occurrence of small eyespots is most frequent among Neotropical butterfly groups that feed on or near the ground in forest habitats, these being the Morphinae, Brassolinae, and Satyrinae.

In general, there is a burst of butterfly feeding activity just before sunset on clear, sunny days in Costa Rican lowland tropical rain forests (pers. obs.). While sections of the forest floor receive varying amounts of direct sunlight during the day and butterflies feeding on rotting fruit sometimes sit in patches of sunlight, Hailman (1977) mentions that Daniel Janzen has noted that direct sunlight is almost horizontal near sunset in tropical forests. Thus near-sunset feeding in butterflies may also occur in patches of direct sunlight. These conditions enhance the visual perception of eyespots by vertebrate predators while the butterflies are feeding.

Some recent data from temperate zone forests indicate that vertebrates that disperse the fallen fruits of some tree species are most active in areas where direct sunlight is more abundant (Thompson and Willson 1978). Damage of fallen fruit by various invertebrates was cited as the major selection pressure favoring rapid dispersal of fruit in that study. Thus, a similar pattern may exist in tropical forests, where light gaps and other types of exposed areas are common. This means that small vertebrates which disperse fruit and are opportunistic predators of butterflies, could be active in sunny places where feeding butterflies maximize exposure of eyespots while feeding.

### Intoxication and Modification of Behavior

Fallen ripe fruits are attacked by a wide variety of microbes, these organisms producing toxins, antibiotics and other mechanisms of substrate degradation that result in fruit spoilage or rotting (many references in Janzen 1977). This rotting or fermentation releases volatile substances that attract

insects, including many Lepidoptera; fermenting fruit juices become available as food for butterflies as the result of seeping through breaks in the fruit wall, or from general seepage through a decaying fruit wall. Rotting fruits and moldy (yeasty) sap flows are common sources for the isolation of yeasts, which are specialists on eating ripe fruit (Janzen 1977), this interaction forming the basis for feeding by butterflies. While the spoilage of the fruit makes it less available to vertebrates, it becomes a major resource for butterflies.

It is not known exactly what kinds of nutrients butterflies obtain from rotting fruits or moldy sap flows, but alcohol is imbibed since some species exhibit intoxicated behavior after feeding (e.g., Gomez 1977). There are far more observations of occasional intoxication of birds and mammals from feeding on rotting fallen fruits, rendering them easier to capture (Janzen 1977). Owing to the high humidity of the lowland tropical rain forest and the relatively small body size (and nervous system) of insects, it is likely that intoxication in butterflies is more widespread than for larger animals exploiting these food sources. Adults of *Morpho peleides* with abdomens prodigiously distended and swollen, as the result of extended periods of feeding at baits of rotting bananas, are unable to fly away when disturbed (pers. obs.). In some instances where feeding is less intense at baits, adults fly away but with great difficulty, making them very easy to capture with a net (pers. obs.). My experience with bait studies of *Morpho* and *Caligo* in Costa Rica from 1968 through 1976 is that the longer adults are left undisturbed feeding at these fruits (usually bananas) the greater the level of apparent intoxication as reflected in the impairment of typical escape behavior. Butterflies, when recently arrived at a bait and disturbed, do not exhibit such modified behavior, presumably because there has been insufficient feeding for intoxication to occur. When intoxicated butterflies such as *Morpho* and *Caligo* are picked up, they excrete large quantities of fluid; when left undisturbed for a period, most fluids are excreted and eventually these individuals "sober up" and fly away.

For morphos and brassolines the sequence of events in typical escape behavior elicited when they are deliberately disturbed, shortly after arriving at a bait, is a brief period of rapid, jerky wing movements followed by walking and flight. When disturbed following considerable feeding, the behavioral sequence is to remain motionless and then an attempt to fly away. In some instances, a heavily intoxicated *Morpho peleides* remains motionless even after an aerial net is placed over it. As with other animals, symptoms of intoxication in butterflies include the tendency to sit quietly, apparently the result of depression of the nervous system. A consequence is that recovery time is extended and it is this interruption of the typical escape behavior that renders intoxicated butterflies easy prey for vertebrates.

Intoxicated butterflies are frequently discovered at fruit baits deliberately

placed in small piles on the forest floor (e.g., Young 1972a; 1973; Young and Thomason 1974) whereas butterflies observed at natural food supplies are seldom intoxicated (e.g., Young 1975). Therefore, the frequency of severe intoxication under natural conditions is questionable. Introduced baits, several centimeters across and placed close-by in an area represents a highly available food supply as most natural supplies come in smaller patches and the patches are very dispersed. Thus although the fallen fruits of *Coumarouna* trees are abundant seasonally and attract *Morpho amathonte*, *Morpho peleides*, and many satyrines, the sweet-smelling pulpy cover on each fruit occurs as a thin coat and this coat generally dries up in a few days. Other natural food supplies include small, yeasty fresh sap flows at the base of large forest trees (Young 1975) attracting *Morpho* and several Satyrinae.

The single exception to these observations would be the availability of large quantities of rotting banana (*Musa* (Musaceae)) in plantations, and areas where there are extensive plantings of other fruit trees such as mango (*Mangifera* (Anacardiaceae)) and guava (*Psidium* (Myrtaceae)). In these habitats, large quantities of rotting fruit are available to butterflies for several months each year, and intoxicated individuals of *Morpho* and *Caligo* have been seen (pers. obs.).

### Patterns of Butterflies at Fruits

As the result of capture-mark-resight field studies, it has been found that by far the majority of individuals appearing at both experimental and natural rotting fruits and moldy sap flows for *Morpho*, *Caligo* and several satyrines (e.g., *Antirhea*, *Piriella*, *Caerois*, *Taygetis*) are males (Young 1972a; Young 1973; 1975; Young and Muyschondt 1973; Young and Thomason 1974; pers. obs.). Females tend to show up more irregularly than males (Young 1972a). The scarcity of females at natural food supplies in forest habitats is less understood. But Young and Thomason (1974) found that females of *Morpho peleides* were far less abundant than males at fallen fruits of *Guazuma ulmifolia* Lam. (Sterculiaceae). A similar pattern of abundance between the sexes was seen on the sap flows of *Samanea saman* Merrill (Leguminosae) for the same population at a different time (Young 1975). The sex ratio of laboratory-reared *Morpho peleides* is unity (Young and Muyschondt 1973). It seems, therefore, that for at least *Morpho peleides*, there is a definite behavioral difference in feeding activities between males and females. The observed general tendency for males to predominate at bait for several species of satyrines and brassolines in addition to morphos, suggests that such a behavioral difference is widespread among these butterflies, although more data are needed to confirm this prediction.

In addition to the above considerations in relation to feeding, eyespots undoubtedly function to enhance survival from predators while butterflies



are resting. As with feeding on the ground, morphos, satyrines, and brassolines generally spend the night hanging from leaves near the ground (pers. obs.). During these periods the butterflies are exposed to nocturnal vertebrate predators such as lizards and small mammals.

### Discussion

Although many insects including some nymphalines of temperate zones exploit rotting fruits and moldy sap flows (e.g., Simon and Enders 1978), such feeding behavior is more prevalent in the American tropics, where members of four major subfamilies of nymphalids, the Nymphalinae, Morphinae, Brassolinae, and Satyrinae (following Ehrlich 1958), contain genera and species whose adults feed almost exclusively upon these food sources. While it is known that some temperate-zone families of Lepidoptera are attracted to volatile fermentation products (e.g., Utrio and Eriksson 1977), less is known about the attraction of tropical butterflies to rotting fruits and moldy sap flows. Bait studies indicate that butterflies become intoxicated from extended periods of feeding on an abundant fruit supply and fruit products (i.e., large resource patch). Although intoxication is less likely for butterflies exploiting natural food sources which tend to be smaller and dispensed in space and time, it is expected that some individuals of a species would experience intoxication, thus increasing the likelihood of being detected by predators. In addition to insects being attracted to these food sources, vertebrate predators may also be attracted to rotting fruit and moldy sap flows. Such conditions favor the evolution of morphological crypsis and associated behavior patterns that provide effective passive protection of intoxicated individuals.

Although the functional role of eyespots on the undersides of lepidopteran wings has been examined (e.g., Stradling 1976), I wish to advance a new hypothesis to account for the adaptive role of these markings. The small eyespots so familiar on many different species of satyrines, brassolines, and morphines, and the noticeable lack thereof in most nymphalines (including fruit and sap-feeding forms) suggests that they function to provide additional protection for butterflies feeding from the forest floor; butterflies generally feeding arboreally, including most nymphalines that feed on moldy sap flows, lack eyespots, suggesting that such markings are less adaptive to butterflies in these feeding niches. Owing to the increased likelihood that rotting fruits have already fallen from the parent tree by the time they are degraded to suitable food for butterflies, most incidents of intoxication probably occur on the forest floor. Here, the eyespots (Fig. 1) provide additional protection to an individual butterfly that perhaps is partially intoxicated to a point of impairment of escape behavior. If such markings act as effective decoys for pecking by birds and flash attacks by other vertebrate predators, they provide additional time for an escape.

Owing to the close evolutionary history of the Satyrinae, Brassolinae, and Morphinae (Miller 1968), eyespots probably evolved in one of these groups and were then carried over to the others as they evolved. It is less clear as to how these markings, so strikingly similar among most members of these three groups, could have also evolved in the Nymphalinae, a very large group exhibiting manifold patterns of resource exploitation, both as larvae and adults. Most members of the Morphinae as well as all members of the Satyrinae and Brassolinae are monocot-feeders as larvae (Ehrlich and Raven 1965; Miller 1968). Virtually all Nymphalinae are dicot-feeders (Ehrlich and Raven 1965). Although it is difficult to determine whether or not the Brassolinae and Satyrinae were derived phylogenetically from the Morphinae, or the reverse (e.g., Young 1972b; Ehrlich and Raven 1965; Durden and Rose 1978), the three groups are closely linked in evolutionary history.

The collections of fallen, rotting fruits available each year in the tropical wet forests are a major food resource for many butterflies, and the abundance and local diversity of these insects may be determined in part by these resources. The various sweet-smelling to fermenting odors given off by these fruits attract butterflies and other insects, and the activities of these animals in turn hasten the decay processes, making the fruit less attractive to larger animals (Janzen 1977). In terms of the insects, the fruits are a predictable resource in time and space and such predictability may be a major selective factor in the establishing of breeding populations of individual species in a region of tropical forest. The repeated exploitation of a fruit crop in an area by the subset of the butterfly community that feeds on fruits reduces the likelihood that these fruits will be carried away from the area by larger animals acting as dispersal agents. As discussed primarily for microbes associated with rotting fruit (Janzen 1977), the butterflies and other insects are entering a competitive interaction with larger animals for this food supply. Such interactions are less likely at arboreal sap flows, although both resources are probably limiting factors for butterflies. Thus the likelihood that opportunistic predators on large insects (reptiles, birds, and small mammals), will be active near or at fruits on the forest floor is greater than for arboreal sap flows; such conditions select for behavior and morphological adaptations that increase the survival of the butterflies feeding on the fruits.

Eyespot markings have high adaptive value under these conditions, and females are less abundant in such places since males are the more expendable. If mortality of feeding butterflies is high, selection favors more cryptic behavior in females. Although the high levels of intoxication of butterflies at fruit baits and fruit products (e.g., Gomez 1977) are probably not frequently attained in nature, save for the exploitation of fallen fruit in banana plantations, there exists a spectrum of intoxication levels affecting escape behavior. Breakage of the wall of a fruit by rotting, falling, or handling by

animals allows fruit-foraging butterflies to use the fruit as a food source, but at the same time it exposes a portion of the population to intoxication which in turn lowers fitness. This interaction is mediated by the microbe community associated with the fruit. As discussed primarily for the microbes (Janzen 1977), the joint activities of dispersal agents (vertebrates) affects fitness in the populations of the plant (tree) species involved.

The ideas developed in this paper on the adaptive significance of butterflies feeding on rotting fruits and fermenting sap flows in the tropics may also be applicable to the temperate zone fauna. For nymphalids of the temperate zone that feed on sap flows and only occasionally on rotting fruit, there is a lack of eyespot markings. Most of these feed arboreally and the density of vertebrate predators is very likely lower than in comparable tropical habitats. Selection pressures favoring eyespots are expected to be most intense in the tropics, and to be most prevalent among butterflies that feed on rotting fruits on the forest floor. Given the great diversity of butterflies in the tropics, the occurrence of eyespots in three large groups, such adaptations may have high selective value hitherto underemphasized.

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Received for publication July 31, 1978.